

DISTRIBUTION AND ENVIRONMENTAL PREFERENCES OF DEEP SEA BENTHIC FORAMINIFERA IN THE PANAMA BASIN, EASTERN PACIFIC OCEAN

Distribución y preferencias ambientales de los foraminíferos bentónicos de aguas profundas de la cuenca de Panamá, Pacífico Oriental

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ABSTRACT

The Recent benthic foraminiferal families Bolivinidae, Buliminidae and Uvigerinidae from 34 core top samples were studied in order to analyze their geographic distribution and possible environmental controls in the Panama Basin. A cluster analysis defined five assemblages based on the percentage abundance of 33 species. The Bolivinidae and Buliminidae have a homogeneous distribution along the basin, in comparison to the Uvigerinidae, which has its largest proportion over the western flank of the Cocos Ridge and over the north-western flank of the Carnegie Ridge. A canonical correspondence analysis (CCA) over 26 species suggests that the Bolivinidae and Buliminidae are related to bottom temperature, in comparison to the Uvigerinidae, which has a more complex relation with depth, salinity and dissolved O₂ content.

Key words. Ecology, Deep sea sediments, Panama Basin, Recent benthic foraminifera.

RESUMEN

Se analizaron las familias de foraminíferos bentónicos recientes Bolivinidae, Buliminidae y Uvigerinidae presentes en 34 muestras superficiales (*core top*) en la cuenca de Panamá, con el fin de determinar su distribución geográfica y posibles controles ambientales. Un análisis de agrupamiento (*cluster*) permitió definir cinco asociaciones basadas en las abundancias porcentuales de 33 especies pertenecientes a estas familias. Las familias Bolivinidae y Buliminidae presentan una distribución homogénea a lo largo y ancho de la cuenca, a diferencia de las especies de la familia Uvigerinidae, las cuales presentan sus mayores abundancias porcentuales en el margen occidental de la dorsal de Cocos y en el flanco nororiental de la dorsal de Carnegie. Un análisis de correspondencia canónica (CCA) efectuado para 26 especies sugiere que las familias Bolivinidae y Buliminidae presentan una relación con la temperatura de fondo. Por otro lado, la familia Uvigerinidae presenta una relación más compleja con la profundidad, la salinidad y el contenido de O₂ disuelto.

Palabras clave. Cuenca de Panamá, Ecología, Foraminíferos bentónicos recientes, Sedimentos de aguas profundas.

INTRODUCTION

The foraminifera (Granoreticulosidae-Foraminiferida) are a highly successful and diverse protist group with a wide distribution in the oceans (e.g. Sen Gupta 1999). In the fossil record, deep-sea benthic foraminifera are the organisms with the highest preservation potential. (e.g. Gooday *et al.* 1992, Gooday 1994). Therefore, the study of their assemblages, together with the analysis of their isotopic or geochemical composition have contributed to the reconstruction of the paleoceanographic and paleoclimatic conditions of the Mesozoic-Cenozoic eras (e.g. Loubere 1994, Sen Gupta 1999, Murray 2006, Jorissen *et al.* 2007).

The Panama Basin, which is located in the northeastern equatorial Pacific, is bounded by the Cocos and Carnegie Ridges, and is crossed by the Coiba and Malpelo Ridges, which divide the basin into a deeper western and a shallower eastern region (Figure 1). Sub-surface water masses in the basin belong to the Antarctic Intermediate Water (AAIW) which reaches a water depth of around 1500 m, and the Lower Circumpolar Deep Water (CDW) which crosses the basin in its deeper parts (>3000 m). Both water masses present similar physical properties, i.e. a salinity of 34.6 psu, a temperature of 2-3°C, and a dissolved oxygen content of 0.8-2.9 ml/l (Fiedler & Talley 2006). They travel along the western margin of southern South America and move across the Ecuador-Colombia trench to reach the western Panama Basin. This, they do either, at the southern depression of the Malpelo Ridge, or between the Coiba and Malpelo Ridges. Finally, they leave the basin westward in response to the dynamics of the equatorial currents (Laird 1971, Lonsdale 1976, Fiedler & Talley 2006). Numerous studies have dealt with variations in the physical properties of these water masses in the Panama Basin during Quaternary period, mainly due to its strategic paleoceanographic location in the

world ocean. Studies based on benthic and planktonic foraminiferal assemblages have reconstructed the paleoceanography of the Panama Basin since the Pliocene period (e.g. Betancur & Martínez 2001, Loubere 2002, Koutavas *et al.* 2002, Martínez *et al.* 2003, 2006, Benway *et al.* 2006, Ovsepian & Ivanova 2009). Despite these efforts, the definition of climate models in the Equatorial Pacific, i.e. El Niño like vs La Niña like during the Last Glacial Maximum is still controversial (e.g. Koutavas *et al.* 2002, Martínez *et al.* 2003). In addition, the geochemical proxies based on benthic foraminifera (e.g. Mg/Ca, $\delta^{18}\text{O}$, $\delta^{13}\text{C}$) and their interpretations depend on an accurate knowledge of benthic foraminiferal ecology (e.g. Jorissen *et al.* 2007). Therefore, it is important to study which biologic and physicochemical components control the deep-sea benthic assemblages in order to improve future paleoceanographic interpretations in the Eastern Equatorial Pacific.

This work explores the composition of three common benthic foraminiferal families (Bolivinidae, Buliminidae and Uvigerinidae) in the Panama Basin using a cluster analysis. A canonical correspondence (CCA; ter Braak & Verdonschot 1995) analysis was performed in order to better comprehend if environmental variables such as temperature, dissolved oxygen, salinity and depth could influence the occurrence of these three benthic foraminifera families in the basin.

MATERIALS AND METHODS

We present the relative abundance (percentage) of benthic foraminiferal species recovered from the 0-1 cm interval of 34 core-top sediment samples from the Panama Basin (Figure 1; Table 1). These include previous data plus a new dataset (15 new samples) from the KN176-2 (<http://dlacrisedata.whoi.edu/KN/KN176L02/index.php>), and the AMADEUS (Collot *et al.* 2002) research cruises. These samples, ~5 g in weight,

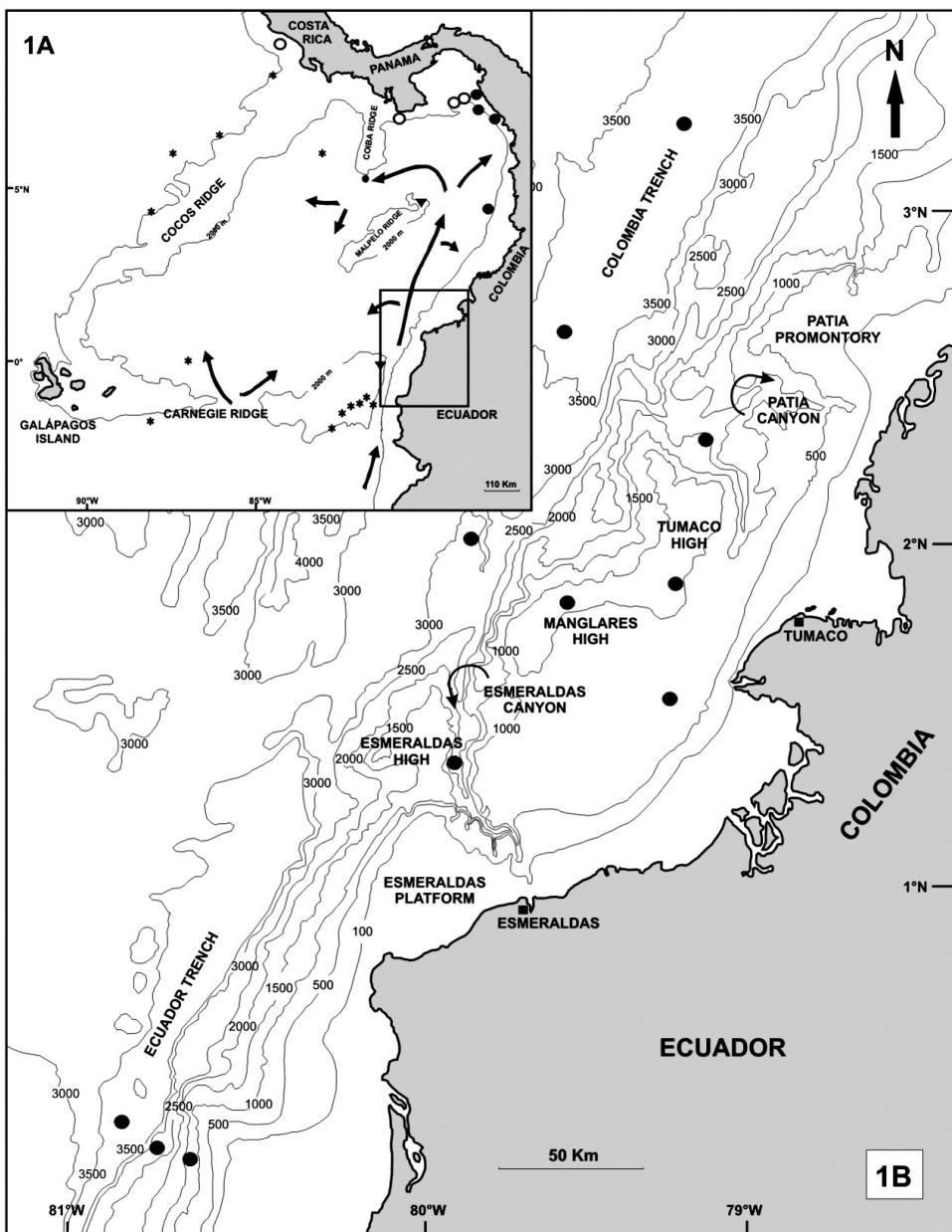


Figure 1. Sample location and bottom current (arrows), Panama Basin (modified from Laird 1971, Lonsdale 1977, Collot *et al.* 2002).

Note the sample distribution in 1A-B: • this work; * Betancur & Martínez 2003, ○ Bandy & Arnal 1954, ▼ Bandy & Rodolfo 1964.

Table 1. Percentage abundances of the main species of the Bolivinidae, Buliminidae and Uvigerinidae families from core-top samples from the Panama Basin. Species used in the CCA are indicated by the gray color shade.

were washed with water using 63 and 150 μm sieves, and dried at room temperature. About 100-300 specimens per sample were collected of the $>150 \mu\text{m}$ and 63-150 μm fractions in each sample, and then counted and identified. This, in order to incorporate data from 19 samples previously studied by Bandy & Arnal (1957), Bandy & Rodolfo (1964) and Betancur & Martínez (2003). Future work will hopefully be carried out using unsieved samples. The sample set we used has a distribution that ranges from the middle upper bathyal (500-1500 m), the middle lower bathyal (1500-2000 m), and the lower bathyal (2000-4000 m).

Generic classification of foraminifera was based on taxonomy keys (Revets 1996, Loeblich & Tappan 1964, Seiglie 1969) and previous reports from the Panama Basin (Bandy & Arnal 1957, Smith 1963, 1964, Bandy & Rodolfo 1964, Golik & Phleger 1977, Gualancañay 1986, Betancur & Martínez 2003). Environmental variables such as temperature, dissolved oxygen and salinity were obtained from the World Ocean Atlas 2009 database (WOA09; <http://iridl.ledee.columbia.edu/SOURCES/.NOAA/.NODC/.WOA09/>) using the depths and geographic locations of each sample. The WOA09 database presents general trends because it is a compilation of the annual average of each physicochemical variable for a number of years.

Grouping of the three studied benthic foraminifera families was conducted with a cluster analysis using the MVSP 3.1 software (*Multi-Variate Statistical Package*), and applying the hierarchical agglomerative method of the Ward's minimum variance. This method allows the clustering of the data with a lower increment of variance between each pair of samples (Legendre & Legendre 1998).

Correlation between foraminiferal species and physicochemical variables was effectuated

by a Correspondence Canonical Analysis (CCA) using the same statistical software. CCA determinates close relations between species assemblages and environmental descriptors by making direct comparisons between these data matrices. This method can be applied to presence-absence and species abundance matrices (ter Braak & Verdonschot 1995, Legendre & Legendre 1998). To avoid anomalous results when species abundances are low or close to zero, we selected only those species with percentage values $\geq 2\%$ of total abundance, and occurring in more than two samples. In addition, a logarithmic transformation was conducted to avoid contractual values (ter Braak & Verdonschot 1995).

RESULTS

The identified benthic foraminiferal species belong to the families Bolivinidae (genera *Bolivina* and *Brizalina*), Buliminidae (genera *Bulimina* and *Globobulimina*) and Uvigerinidae (genus *Uvigerina*). A total of 33 species distributed in 34 samples were analyzed using cluster analysis, with a ≤ 2.0 squared Euclidian distances. This dataset allowed us to define five assemblages (Table 1; Figure 2), which are described as follows:

Assemblage I: Composed of *Globobulimina affinis*, *Globobulimina pacifica* and *Globobulimina* sp. as representative species (samples KAMA 21 and KAMA 24). Samples of this assemblage are located northwest of the Carnegie Ridge, over the middle and distal part of the Esmeraldas River submarine canyon (Collot *et al.* 2002).

Assemblage II: Composed of *Brizalina argentea*, *Bolivina humilis*, *Bolivina* sp. and *Globobulimina* sp. as representative species (eight samples). Almost all samples are located between 0-2° North on the upper-lower middle bathyal zones of the Colombian Pacific platform. Two samples with the same foraminiferal assemblages are located on the northeastern part of the Panama Basin, near

the continental slope (samples JPC-9 and MC-21B).

Assemblage III: *Uvigerina mantaensis*, *Uvigerina proboscidea* and *Uvigerina vadescens* are the representative species of this assemblage (six samples). The latitudinal distribution of this assemblage is quite variable around the entire basin. This assemblage is located in the lower-middle and the lower bathyal zone on the western margin of the Cocos Ridge (82° West), the middle part of the Carnegie Ridge, and the Panama Gulf (samples TR163-33 and H37).

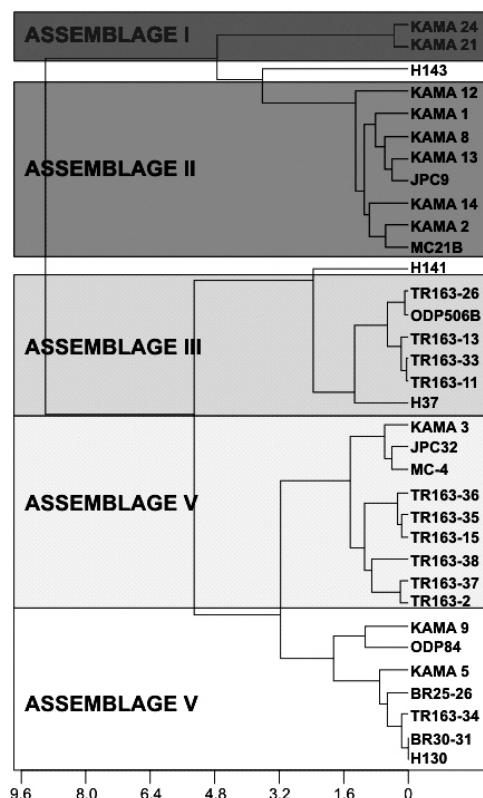
Assemblage IV: It includes *Uvigerina hispida*, *Uvigerina hispidocostata* and *Bulimina striata* as the most representative species, with a lower proportion of *Uvigerina proboscidea* (nine samples). Like Assemblage III, this assemblage has a wide latitudinal distribution. Although most the samples are located in the lower-middle and the lower bathyal zones of the northeastern part of the Carnegie Ridge, some are located over the western flank of the Cocos Ridge and the eastern-central part of the Panama Basin (samples TR163-15, TR163-2, JPC-32, and MC-4).

Assemblage V: It includes a mixed composition of species from previous assemblages (e.g. *U. mantaensis*, *U. proboscidea*, *Globobulimina pacifica*), but in proportions lower than 10% (seven samples). Assemblage V is located in the upper-middle and lower bathyal zones between $2-6^{\circ}$ North, except for samples H130, BR30-31 and TR163-34, which belong to the Panama Gulf and the northeastern part of the Carnegie Ridge.

Samples H141 and H143, located on the northeastern part of the Panama Basin, have foraminiferal compositions that do not match with the proposed assemblages. According to the squared Euclidian distance (> 3.5), sample H143, which it is placed between assemblages I and II, could be more similar to assemblage II. Both assemblages present common species such as *Bolivina* sp., but there are some differences in the proportions

of particular species such as *Uvigerina peregrina* and *Uvigerina excellens*. According to the CCA, sample H141 could be also related with samples of assemblage III. The high abundance of *Uvigerina vadescens* (30%) in sample H141 could explain this relation.

Minimum variance



Euclidian distance (Log10 transformed)

Figure 2. Dendrogram of the 34 analyzed core-top samples from the Panama Basin using the minimum variance method.

In the CCA analysis, as in the cluster analysis, we used a matrix of 26 species, i.e. only those species with abundances $\geq 2\%$ and those found in more than two samples (Figure 3; Tables 1, 2). Cumulative percentages in axes 1 and 2 explain 23.6% and 36.9% of the total variance, respectively. Environment-species correlations were 1 and 0.99 to axis 1 and

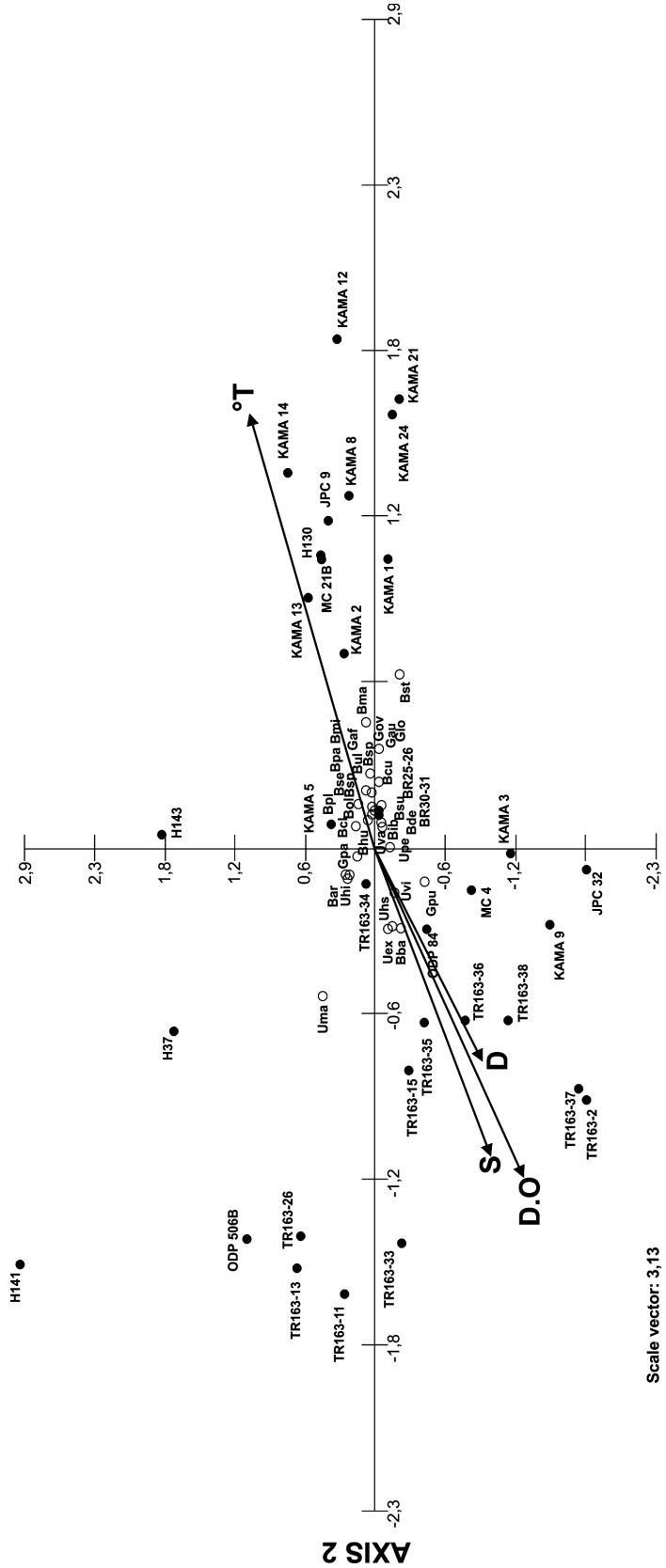


Figure 3. CCA diagram illustrating the relation of 26 benthic foraminiferal species and environmental variables such as temperature ($^{\circ}\text{T}$), salinity (S), dissolved oxygen (D.O) and depth (D) in the Panama Basin. (\rightarrow = environmental variables, \circ = samples, \bullet = species). Bhu= *B. humilis*, Bse= *B. seminuda*, Bsp= *B. semiperforata*, Bsu= *B. subadvena*, Bol= *Bolivina sp.*, Bar= *B. interjuncta bicostata*, Bcl= *B. argentea*, Bib= *B. clava*, Bde= *B. denudata* Bst= *B. striata*, Bcu= *B. curta*, Bul= *Buliminella sp.*, Gaf= *G. affinis*, Gau= *G. auriculata*, Gov= *G. ovula*, Gpu= *G. pacifica*, Gpu= *G. pupoides*, Glo= *Globobulimina sp.*, Uex= *U. excellens*, Uhi= *U. hispida*, Uhs= *U. hispidocostata*, Uma= *U. mantaensis*, Up= *U. proboscidea*, Upe= *U. peregrina*, Uvi= *U. vadezensis*, Uvi= *Uvigerina sp.*

2, respectively (Table 3). Temperature is the variable that better explains the ordering in the species in axis 1, with a canonic coefficient of 0.61. On axis 2 the variable that better correlates is salinity with a canonic coefficient of -1.45 (Table 4). A Monte Carlo permutation test (1000 permutations) resulted in a positive value ($p = 0.05$), suggesting a non-random distribution of data in the CCA. *Uvigerina proboscidea* (Upr; Figure 3) and *U. hispida* (Uhi) are the most frequent species in all the samples (Table 1), suggesting a cosmopolitan distribution in the Basin.

The CCA diagram shows that 50% of grouped species belonging to the *Bolivina* and *Globobulimina* (except *G. ovula*; Gov) genera present an apparent relation with temperature. Relative abundances of *U. excellens* (Uex), *Uvigerina* sp. (Uvi), *B. clava* (Bcl), *U. peregrina* (Upe) and *U. vadescentes* (Uva) do not show any apparent relation with the four analyzed variables, though they are properly represented in the subspace of canonic axis 1 and 2. Therefore, the presence of these taxa could be explained by more than one physicochemical variable

Table 2. Sample location (core-tops), and environmental variables (annual average) from the World Ocean Atlas 2009 in the Panamá Basin <http://iridl.ideo.columbia.edu/SOURCES/NOAA/NODC/.WOA09/>.

Samples	Coordinates	Depth (m)	Dissolved oxygen (ml/l)	Temperature (°C)	Salinity (psu)
H130	9,15°N 84,15°W	1246	1,2006	3,7366	34,5963
TR 163-2	8,24°N 84,3°W	1620	1,9264	2,528	34,6207
MC 21B	7,51°N 77,7°W	1065	1,12035	4,6046	34,5759
MC 4	7,27°N 78,24°W	2121	2,023	2,3339	34,6502
H143	7,10°N 80,47°W	1025	1,0005	4,7577	34,5753
H37	7,10°N 78,30°W	1400	1,4413	3,3507	34,6047
JPC 9	6,82°N 77,9°W	2888	2,5141	2,0258	34,6742
TR 163-11	6,45°N 85,8°W	1950	2,2459	2,2758	34,6489
H141	6,45°N 81,0°W	1912	1,8536	2,4753	34,6502
TR 163-13	6,03°N 87,4°W	2450	2,524	1,9048	34,6649
ODP 84	5,75°N 82,9°W	3096	2,4859	2,037	34,6677
JPC 32	4,67°N 77,96°W	2195	2,25085	2,3427	34,66
TR 163-15	4,27°N 87,9°W	1770	2,0678	2,5982	34,6336
BR25-26	4,21°N 85,7°W	2489	2,442	2,073	34,6654
KAMA 5	3,15°N 79,11°W	3700	2,7759	1,9824	34,6772
KAMA 9	2,39°N 79,32°W	3550	2,7655	1,9958	34,6692
KAMA 8	2,21°N 79,08°W	1335	1,2585	3,4957	34,5931
KAMA 21	2,02°N 79,5°W	2954	2,7199	1,9681	34,6672
KAMA 13	1,54°N 79,13°W	714	0,8001	6,3107	34,5714
KAMA 12	1,51°N 79,31°W	815	1,1603	5,6175	34,6114
KAMA 14	1,34°N 79,14°W	784	1,1603	5,9641	34,5935
KAMA 24	1,22°N 79,52°W	1623	1,8727	2,947	34,6335
ODP 506B	0,61°N 86,1°W	2711	2,4687	2,089	34,6666
KAMA 3	0,19°N 80,5°W	3797	2,9069	1,9094	34,6774
KAMA 1	0,17°N 80,43°W	3046	2,7632	1,921	34,673
KAMA 2	0,13°N 80,39°W	1315	1,6327	3,6006	34,5993
BR30-31	0 °N 81,4°W	1180	1,581	3,959	34,5956
TR 163-34	1,31°S 81,9°W	1360	1,7983	3,5036	34,616
TR 163-38	1,34°S 81,6°W	2200	2,5594	2,0745	34,6561
TR 163-35	1,35°S 81,9°W	1415	1,8946	3,3764	34,6231
TR 163-37	1,35°S 81,7°W	2005	2,3549	2,3249	34,6494
TR 163-36	1,36°S 81,8°W	1780	2,2417	2,626	34,6398
TR-163-26	1,89°S 87,8°W	3000	2,879	1,925	34,6701
TR 163-33	1,91°S 82,6°W	2230	2,3336	2,3085	34,6642

(e.g. nitrates); alternatively, these species may not be representative in slope sediments. The abundance of *B. striata* (Bst), *U. hispidocosta* (Uhs), *U. proboscidea* (Upr), *U. mantaensis* (Uma), and *U. hispida* (Uhi) is probably related to depth, salinity and dissolved O₂, suggesting that these species could be tolerant to modifications in these variables.

Table 3. Estimated eigenvalues of the CCA for the analyzed core-top samples of the Panama Basin.

Eigenvalues	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0,035	0,02	0,018	0,015
Percentage	23,601	13,287	12,26	10,357
Cummulative percentage	23,601	36,888	49,149	59,506
Species-environments correlations	1	0,999	1	0,998

Table 4. Canonical coefficients for the analyzed variables according to the main four axis of the CCA.

Environmental variables	Species-Axis 1	Species-Axis 2	Species-Axis 3	Species-Axis 4
Depth	0,085	1,025	-0,183	-1,55
Dissolved oxygen	-0,251	0,282	-0,053	-0,089
Temperature	0,612	-0,368	-0,241	0,875
Salinity	0,341	-1,448	0,15	2,105

Sample distributions in the CCA analysis suggest similar patterns between the assemblages as proposed by the cluster analysis. Assemblage I, which occurs in samples KAMA 21 and KAMA 24, is observed in the canonic subspace of axis 1. Conversely, samples that do not group in the cluster analysis (H141, H143) cannot be defined in the CCA analysis. Sample H141 does not follow any of the vectors (variables) of the CCA, thus showing the largest distance with respect to the origin of canonic axes 1 and 2. Samples bearing assemblage II can be explained by temperature, while samples bearing assemblage III are well represented in the canonic subspace of axis 2, but do not show any apparent relation with the analyzed variables. Samples bearing assemblage IV have an apparent relation with depth, salinity and dissolved O₂. Finally, assemblage V

that has some of its samples (e.g. BR30-31 and BR25-26) lying at the center of the diagram, do not show any ordering along the analyzed variables (Figure 3). Therefore, this assemblage cannot be explained by any of the variables considered in the CCA.

DISCUSSION

Since species of the Bolivinidae family have a wide distribution along the Panama Basin, they do not define any of the proposed assemblages in the middle and lower-upper bathyal zones, showing an apparent relation with temperature in the CCA. However, assemblages of the Bolivinidae have been used to characterize biofacies in slope zones along Central America and the Equatorial Pacific (e.g. Smith 1964, Golik & Phleger 1977).

On the other hand, the distributions genera of the Buliminidae present mixed results. In general, the abundance of *Bulimina* is low and its species composition in the studied samples is quite homogeneous. Therefore, many of the species of this family do not show a clear pattern in the CCA and cluster analysis, and only *B. striata*, a common species in assemblage III, has an apparent relation with salinity, dissolved O₂ and depth. In contrast, the genus *Globobulimina*, which is characteristic of assemblage I, is possibly related to bottom temperature according to the CCA. Assemblage I is located near the submarine canyon of the Esmeraldas River, where sediment transport could control the composition of the Bolivinidae, Buliminidae and Uvigerinidae families, giving an apparent ecologic advantage to the genus *Globobulimina*. This genus is detritivorous, infaunal, and is related to poorly oxygenated mud (e.g. Rathburn & Corliss 1994, Fontanier *et al.* 2002, Murray 2006). Since episodic transport of terrigenous material is expected from the submarine canyon of the Esmeraldas River, the predominance of *Globobulimina*

could be explained by: (1) low sedimentation rates of terrigenous material or, (2) a different variable such as phytodetritus or other nutrients supplied by the Esmeraldas River (cf. Gómez & Martínez 2005).

According to the cluster analysis, the distribution of the Uvigerinidae is more abundant in the western margin of Panama Basin on the Cocos Ridge (assemblage III) and the northeastern flank of the Carnegie Ridge (assemblage IV). This result corroborates previous observations in the northwestern part of the Panama Basin, where these species have been suggested to be highly adapted to extreme productivity and low O₂ concentrations in the sediments (Ovsepian & Ivanova 2009). In addition, the presence of some particular species of the Uvigerinidae family could be explained by the dissolved O₂, salinity and depth. For instance, *U. peregrina* is a common species in high productivity systems with constant nutrient concentrations in the oxygen minimum zone (OMZ; e.g. Fontanier *et al.* 2002, Ovsepian & Ivanova 2009), which in the Panama Basin can reach the 800 m water depth (Fiedler & Talley, 2006). However, the detected variation in composition and distribution of the Uvigerinidae could respond to a highly complex environmental habitat. This is the case of *U. proboscidea*, a species that inhabits environments with variable temperature and intermediate oxygen content (e.g. De & Gupta 2010). Such variability could be expressed by: (1) variations in the oxygenation conditions related to the displacement of the CDW across the Panama Basin (Gualancañay 1986) or, (2) low values of dissolved O₂ (1.7-2.6 ml/l) in the southern part of the basin that probably reflect a low input of terrigenous material in the area and affecting the surface productivity (Fiedler & Talley, 2006). Finally, the two areas where assemblages III and IV are located are defined by Betancur & Martinez (2003) as the south eutrophic and middle mesotrophic zones, using benthic foraminiferal assemblages.

Ecologically, a complex setting could be inferred for this part of the Panama Basin.

CONCLUSIONS

Multivariate analyses (cluster and CCA) applied to 34 core-top sediment samples of the Panama Basin suggest that the geographic distribution of the Bolivinidae and Buliminidae families is homogenous along the basin, but presents an apparent relation with bottom temperature. In contrast, species of Uvigerinidae present high abundances along the western margin of the basin on the Cocos Ridge (assemblage III), and the northeastern flank of the Carnegie Ridge, probably explained by depth, salinity and dissolved O₂. Finally, a cluster analysis using the percent abundances of 33 species allowed the definition of five assemblages for the Panama basin, which also were detected in the sample distribution performed by the CCA analysis.

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LITERATURE CITED

- AKIMOTO, K. 1990. Distribution of recent benthic foraminiferal faunas in the Pacific of Southwest Japan and around Hachijojima Island. *Science Reports of the Tohoku University Sendai (Geology)*, second series 60 (2): 288-291.
- BANDY, O.L. & R.E. ARNAL. 1957. Distribution of Recent foraminifera off west coast of Central America. *AAPG Bulletin* 41: 2037-2053.
- BANDY, O.L. & K.S. RODOLFO. 1964. Distribution of foraminifera and sediments, Peru-Chile trench area. *Deep Sea Research* 11: 817-837.
- BENWAY, H.M., A.C. MIX, B.A. HALEY & G.P. KLINKHAMMER. 2006. Eastern Pacific Warm Pool paleosalinity and climate variability: 0–30 kyr. *Paleoceanography* 21: PA3008, doi:10.1029/2005PA001208.
- BETANCUR, M.A. & J.I. MARTÍNEZ. 2001. Productividad y oxigenación de la Cuenca de Panamá, Pacífico Colombiano, durante el Pleistoceno tardío-Holoceno: el registro de los foraminíferos bentónicos. *Geología Colombiana* 26: 123-151.
- BETANCUR, M.A. & J.I. MARTÍNEZ. 2003. Foraminíferos bentónicos recientes en sedimentos de fondo de la cuenca de Panamá (Pacífico Colombiano), como indicadores de productividad y oxigenación. *Boletín de Investigaciones Marinas y Costeras* 32: 3-18.
- BORNMALM, L. 1997. Taxonomy and paleoecology of Late Neogene benthic foraminifera from the Caribbean Sea and Eastern Equatorial Pacific Ocean. *Fossils and Strata* 41: 1-96.
- COLLOT J-Y., P. CHARVIS, M.A. GUTSCHER & S. OPERTO. 2002. Exploring the Ecuador-Colombia active margin and interplate seismogenic zone. *EOS, Transactions of the American Geophysics Union* 83 (17): 189-190.
- CUSHMAN, J.A. 1927. Recent foraminifera from off the west coast of America. *Scripps Institution of Oceanography Technical Series* 1: 119-188.
- CUSHMAN, J.A. & F.L. PARKER. 1938. Notes on some Pliocene and Pleistocene species of *Bulimina*. *Contributions of the Cushman Laboratory of Foraminiferal Research* 14: 1-74.
- DE, S. & A.K. GUPTA. 2010. Deep-sea faunal provinces and their inferred environments in the Indian Ocean based on distribution of recent benthic foraminifera. *Palaeogeography, Palaeoclimatology, Palaeoecology* 291: 429-442.
- DOUGLAS, R.G. 1973. Benthonic foraminiferal biostratigraphy in the Central North Pacific, Leg 17. *Deep Sea Drilling Project. Initial Reports* 17: 607-672.
- FIEDLER, P.C. & L.D. TALLEY. 2006. Hydrography of the eastern tropical Pacific: A review. *Progress in Oceanography* 69: 143-180.
- FONTANIER, C., F.J. JORISSEN, L. LICARI, A. ALEXANDRE, P. ANSCHUTZ & P. CARBONEL. 2002. Live Benthic Foraminiferal Fauna from the Bay of Biscay: Faunal Density, Composition, and Microhabitats. *Deep-Sea Research I* 49: 751-785.
- GOLIK, A. & F.B. PHLEGER. 1977. Benthonic foraminifera from the Gulf of Panama. *Journal of Foraminiferal Research* 7: 83-99.
- GÓMEZ, M.C. & J.I. MARTÍNEZ. 2005. Nueva productividad en el Océano Pacífico oriental ecuatorial como respuesta al aporte de nutrientes por el río San Juan, sistemas de surgencia costera y polvo atmosférico. *Boletín de Geología UIS* 27 (2): 99-114.
- GOODAY, A.J. 1994. The biology of deep-sea foraminifera: a review of some advances and their applications in paleoceanography. *Palaios* 9: 14-31.
- GOODAY, A.J., L.A. LEVIN, P. LINKE & T. HEEGER. 1992. The role of benthic foraminifera in

- deep-sea food webs and carbon cycling. Pp. 63-91 In G.T. Rowe, G.T. & V. Pariente, V. (eds) *Deep-sea Food Chains and the Global Carbon Cycle*. Kluwer Academic Publishers.
- GUALANCAÑAY, E. 1986. Foraminíferos del Rift de Galápagos. *Acta Oceanográfica del Pacífico* 3 (1): 149-155.
- HASEGAWA, S., R. SPROVIERI & A. POLUZZI. 1986. Quantitative analysis of benthic foraminiferal assemblages from Plio-Pleistocene sequences in the Tyrrhenian Sea, ODP Leg 107. *Proceedings of the Ocean Drilling Program. Scientific Results* 107: 461-478.
- JORISSEN, F.J., C. FONTANIER & E. THOMAS. 2007. Paleoceanographical indicators based on deep-sea benthic foraminiferal assemblage characteristics. *Developments in Marine Geology* 1: 263-325.
- KAIHO, K. 1989. Eocene to Quaternary benthic foraminifers and paleobathymetry of the Izu – Bonin Arc, Legs 125 and 126. *Proceedings of the Ocean Drilling Program. Scientific Results* 126: 285-310.
- KAIHO, K. & A. NISHIMURA. 1989. Distribution of Holocene benthic foraminifers in the Izu – Bonin Arc. *Proceedings of the Ocean Drilling Program. Scientific Results* 126: 311-320.
- KOUTAVAS, A., J. LYNCH-STIEGLITZ, T.M. MARCHITTO JR. & J.P. SACHS. 2002. El Niño-like pattern in ice age tropical Pacific sea surface temperature. *Science* 297: 226–230.
- LAIRD, N.P. 1971. Panama Basin deep water properties and circulation. *Journal of Marine Research* 29 (3): 226-234.
- LEGENDRE, P. & L. LEGENDRE. 1998. *Numerical Ecology*. Second Edition. Elsevier Publishing.
- LOEBLICH, A.R. & H. TAPPAN. 1964. Sarcodina and Foraminifera. In: R.C. Moore (ed.) *Treatise on Invertebrate Paleontology, Part C, Protista*, 2. Lawrence, Kansas University & Geological Society of America.
- LONSDALE, P. 1976. Abyssal circulation of the southeastern Pacific and some geological implications. *Journal of Geophysical Research* 81: 1163-1176.
- LOUBERE, P. 1994. Quantitative estimation of surface ocean productivity and bottom water oxygen concentration using benthic foraminifera. *Paleoceanography* 9: 723-737.
- LOUBERE, P. 2002. Remote vs. local control of changes in eastern equatorial Pacific bioproductivity from the last glacial maximum to the present. *Global and Planetary Change* 35: 113-126.
- MARTÍNEZ, J.I., L. KEIGWIN, T.T. BARROWS, Y. YOKOYAMA, J. SOUTHON. 2003. La Niña-like conditions in the eastern Equatorial Pacific and a stronger Choco jet in the northern Andes during the last glaciation. *Paleoceanography* 18(2): 1033, doi:10.1029/2002PA000877.
- MARTÍNEZ, J.I., D. RINCON, Y. YOKOYAMA & T.T. BARROWS. 2006. Foraminifera and Coccolithophorid Assemblage Changes in the Panama Basin during the Last Deglaciation: Response to Sea-surface Productivity Induced by a Transient Climate Change. *Palaeogeography, Palaeoclimatology, Paleoecology* 234: 114-126.
- MATOBA, Y. & A. YAMAGUCHI. 1982. Late Pliocene to Holocene benthic foraminifers of the Guaymas Basin, Gulf of California: Sites 477 through 481. *Initial Reports of the Deep Sea Drilling Project*, 64, part 2: 1027-1052.
- MOORE, J.R., G.R. HEATH & R.O. KOWSMAN. 1973. Biogenic sediments of the Panama Basin. *Journal of Geology* 81: 458-473.
- MURRAY, J.W. 2006. *Ecology and applications of benthic foraminifera*. Cambridge University Press.
- OHKUSHI, K., E. THOMAS & H. KAWAGATA. 2000. Abyssal benthic foraminifera from Northwestern Pacific (Shatsky Rise) during the last 298 kyr. *Marine Micropalaeontology* 38: 119-147.
- OVSEPYAN E.A. & E.V. IVANOVA. 2009. Benthic Foraminiferal Assemblages as Indicators of the Paleoceanographic Conditions in the

- Eastern Equatorial Pacific. Oceanology 49 (1): 121-129.
- RATHBURN, R. & B.H. CORLISS. 1994. The ecology of living (stained) deep-sea benthic foraminifera from the Sulu Sea. Paleoceanography 9: 87-150.
- REVETS, S.A. 1996. The generic revision of five families of Rotaliine foraminifera. Cushman Foundation for Foraminiferal Research. Special Publication 34: 1-113.
- SEIGLIE, G.A. 1969. Notes on species of the genera *Buliminella* and *Bulimina* (Foraminiferida). Caribbean Journal of Science 9 (3-4): 93-116.
- SEN GUPTA, B. 1999. *Modern Foraminifera* (Second Edition). Kluwer Academic Publishers.
- SMITH, P.B. 1963. Quantitative and qualitative analysis of the Family Bolivinidae. United States Geological Survey Professional Paper 429-A: A1-A39.
- SMITH, P.B. 1964. Ecology of benthonic species: Recent foraminifera off Central America. United States Geological Survey Professional Paper 429-B: B1-B55.
- TER BRAAK, C.J.F. & P.F.M. VERDONSCHOT. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 55 (4): 1-35.
- XIA, T. & Z. FAN. 1996. A study of foraminifera in the core NP93-2 from the Prydz Bay, Antarctica. Antarctic Research 7 (2): 126-140.
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- FAUNAL REFERENCE LIST**
1. *Bolivina humilis*: Matoba & Yamaguchi (1992), p. 1053, pl. 1, figs. 6A-B.
 2. *Bolivina minuta*: Smith (1963), p. A19-20, pl. 30, figs. 11-12.
 3. *Bolivina pacifica*: Smith (1963), p. A16-17, pl. 29, figs. 8-9; Matoba & Yamaguchi (1982), p. 1053, pl. 1, figs. 8-9; Kaiho & Nishimura (1992), p. 318, pl. 3, figs. 15a-b.
 4. *Bolivina plicata*: Revets (1996), p. 23, pl. 1, figs. 7-8.
 5. *Bolivina seminuda*: Smith (1963), p. A15-16, pl. 29, figs. 1-7; Matoba & Yamaguchi (1982), p. 1053, pl. 1, figs. 10-14; Bornmalm (1997), p. 45, fig. 18e.
 6. *Bolivina semiperforata*: Smith (1963), p. A19, pl. 30, figs. 5-8; *Brizalina semiperforata* para Matoba & Yamaguchi (1982), p. 1053, pl. 1, figs. 23-24.
 7. *Bolivina subadvena*: Matoba & Yamaguchi (1982), p. 1053, pl. 1, figs. 15-17..
 8. *Brizalina argentea*: *Bolivina argentea* para Smith (1963), p. A17, pl. 29, figs. 14,17; Matoba & Yamaguchi (1982), p. 1053, pl. 1, figs. 18a-19b.
 9. *Brizalina interjuncta bicostata*: *Bolivina interjuncta bicostata* para Smith (1963), p. A17-18, pl. 30, figs. 1-4; Matoba & Yamaguchi (1982), p. 1053, pl. 1, fig. 21.
 10. *Bulimina barbata*: Kaiho (1989), p. 306, pl. 4, fig. 8.
 11. *Bulimina clava*: Hasegawa *et al.* (1990), p. 476, pl. 3, figs. 16-17.
 12. *Bulimina denudata*: Cushman & Parker (1938), p. 57, pl. 10, figs. 1-2; Smith (1964), pl. 2, fig. 12.
 13. *Bulimina marginata*: Seiglie (1969), p. 111, pl. 4, figs. 8-15; Akimoto (1990), pl. 16, fig. 16; Bornmalm (1997), p. 45, fig. 18i.
 14. *Bulimina spinifera*: *Globobulimina spinifera* para Cushman (1927), p. 151, pl 2, fig. 15.
 15. *Bulimina striata*: Kaiho (1989), p. 306, pl. 4, figs. 3-4; Akimoto (1990), pl. 16, fig. 8; Kaiho & Nishimura (1992), p. 319, pl. 4, fig. 2; Ohkushi *et al.* (2000), p. 140, pl. 2, fig. 3.
 16. *Buliminella curta*: *Buliminella curta curta* para Seiglie (1969), p. 109, pl. 3, figs. 2-18; Matoba & Yamaguchi (1982), p. 1053, pl. 1, fig. 2.
 17. *Globobulimina affinis*: *Bulimina affinis* para Smith (1964), pl. 2, figs. 2-3; Matoba

- & Yamaguchi (1982), p. 1054, pl. 2, figs. 6-7; Kaiho (1989), p. 306, pl. 4, figs. 6-7; Bornmalm (1997), p. 50, figs. 19a-b.
- 18.** *Globobulimina auriculata*: *Bulimina auriculata* para Smith (1964), pl. 2, figs. 4a-b; Bornmalm (1997), p. 50, fig. 19c.
- 19.** *Globobulimina ovula*: Hasegawa *et al.* (1990), p. 476, pl. 3, fig. 18.
- 20.** *Globobulimina pacifica*: Matoba & Yamaguchi (1982), p. 1054, pl. 2, fig. 8; Akimoto (1990), pl. 16, fig. 9; Kaiho & Nishimura (1992), p. 4, fig. 3; Bornmalm (1997), p. 50, fig. 19d.
- 21.** *Globobulimina pupoides*: Akimoto (1990), pl. 16, fig. 16.
- 22.** *Uvigerina ampullacea*: *Uvigerina asperula* var. *ampullacea* para Xia & Fan (1996), p. 139, pl. 1, figs. 14-15.
- 23.** *Uvigerina excellens*: Smith (1964), pl. 2, figs. 13a-b; Matoba & Yamaguchi (1982), p. 1054, pl. 2, fig. 9.
- 24.** *Uvigerina hispida*: Kaiho (1989), p. 306, pl. 4, fig. 9; Akimoto (1990), pl. 16, fig. 11; Akimoto (1990), pl. 16, fig. 16; Bornmalm (1997), p. 50, fig. 19h; Betancur & Martínez (2003), p. 120, pl. 1, fig. 4.
- 25.** *Uvigerina hispidocostata*: Kaiho (1989), p. 306, pl. 4, figs. 10-11; Akimoto (1990), pl. 16, fig. 10; Kaiho & Nishimura (1992), p. 319, pl. 4, fig. 4; Akimoto (1990), pl. 16, fig. 16; Betancur & Martínez (2003), p. 120, pl. 1, fig. 5.
- 26.** *Uvigerina mantaensis*: Bornmalm (1997), p. 50, fig. 19k; Betancur & Martínez (2003), p. 120, pl. 1, fig. 6.
- 27.** *Uvigerina peregrina*: Smith (1964), pl. 2, figs. 15-16; Douglas *et al.* (1973), p. 637, pl. 8, figs. 4-6, 9; Bornmalm (1997), p. 54, figs. 20a-c; Ohkushi *et al.* (2000), p. 140, pl. 2, fig. 4; Betancur & Martínez (2003), p. 120, pl. 1, fig. 7.
- 28.** *Uvigerina peregrina curticosa*: Matoba & Yamaguchi (1982), p. 1054, pl. 2, figs. 10-12.
- 29.** *Uvigerina proboscidea*: Douglas *et al.* (1973), p. 637, pl. 8, fig. 8; Kaiho (1989), p. 306, pl. 4, fig. 12; Akimoto (1990), pl. 22, fig. 12; Kaiho & Nishimura (1992), p. 319, pl. 4, fig. 5; Betancur & Martínez (2003), p. 120, pl. 1, fig. 8; Bornmalm (1997), p. 50, fig. 19f..
- 30.** *Uvigerina vadescens*: Douglas (1973), p. 637, pl. 8, fig. 7; Betancur & Martínez (2003), p. 120, pl. 1, fig. 9.